

Leaf anatomy of Brazilian *Eriocaulaceae* and its diagnostic significance

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Summary

The leaf anatomy of 22 species of *Eriocaulaceae* from Brazil (Federal District of Brasília) was studied by light- and scanning electron microscopy.

For the first time the systematic and taxonomic applicability of the leaf anatomy on generic and infrageneric level is discussed, taking into account own observations as well as results obtained by other investigators.

The leaves of *Eriocaulaceae* show a high degree of variability, in several characters, while in other characters the variability is limited. The latter, for example the absence of certain hair types or the presence of a hypodermis, can be useful for differentiating genera or sections. Others, as the structure of the epidermis cells and the distribution of hairs, may well serve to separate closely related species. In some cases the structure of a certain tissue evidently is influenced by environmental factors.

Generally it is much easier to analyse the anatomy of the leaves than to obtain correct information about the morphology of the tiny floral organs and the habit, which often is diverging due to habitat conditions, even within good species. Additionally to the floral and vegetative morphology the structure of the leaves has proven to be a useful tool for the identification of *Eriocaulaceae*. An identification solely on the basis of the leaf anatomy is generally not possible.

Resumo

Foi estudada a anatomia foliar de 22 espécies de *Eriocaulaceae* do Distrito Federal, Brasil. Pela primeira vez está sendo discutida a aplicabilidade sistemática e taxonômica da anatomia foliar à nível genérico e infragenérico, tomando em consideração estudos particulares e observações de outros investigadores.

As folhas das Eriocauláceas apresentam uma alta variabilidade em muitos dos seus caracteres, como vemos na estrutura das células epidérmicas e na distribuição dos tricomas, que podem servir para separar espécies vizinhas. Outros caracteres têm uma variabilidade limitada, como por exemplo a ausência de certos tipos de tricomas e a presença de uma hipoderme, que pode ser útil para diferenciar gêneros ou seções. Em alguns outros casos a estrutura de certos tecidos foliares parece ser influenciada por fatores ambientais.

Geralmente existe uma maior facilidade em analisar a anatomia foliar do que obter dados corretos sobre a morfologia das flores diminutas e do hábito, que em muitos casos é muito diverso, dependendo das condições ecológicas.

Junto com a morfologia floral e vegetativa, a anatomia foliar mostrou ser extremamente valiosa para a identificação de espécies de Eriocauláceas. Porém, uma identificação somente baseada na anatomia foliar não seria possível.

Key words: Leaf anatomy, taxonomy, *Eriocaulon*, *Paepalanthus*, *Syngonanthus*, *Eriocaulaceae*.

1. Introduction

The *Eriocaulaceae* are a predominantly herbaceous monocotyledon family of 10 genera and approximately 1200 species (HENSOLD & GIULIETTI 1993), of which more than 90% belong to the large genera *Eriocaulon* L., *Paepalanthus* KUNTH, and *Syngonanthus* RUHL.

The *Eriocaulaceae* with few exceptions are pantropical and the two centers of diversity lie in South America (Central Brazil and the Guyana Highlands).

The taxonomy of the *Eriocaulaceae* goes back to RUHLANDS monograph (1903) in which the author included all 470 species known at that time. In spite of various inaccuracies, his system still maintains its validity, because so far no complete revision of the family has been made. After RUHLANDS monograph many smaller monographs and descriptions of new species followed. They all are restricted to certain systematical groups (genera or sections) or geographical regions (RUHLAND 1906; HERZOG 1924, 1931 a, b; SILVEIRA 1918, 1921, HESS 1955, 1957; MOLDENKE & SMITH 1976; GIULIETTI 1978, 1984, 1987; CASTRO 1986; HENSOLD 1988; KRAL 1989; SCATENA 1990). Since 1937 MOLDENKE (e.g. 1949, 1977, 1982) has described a large number of new species, unfortunately in parts incorrectly or incompletely. Thus in many cases his descriptions do not allow a clear identification of species.

The taxonomy of the *Eriocaulaceae* traditionally is

based on characteristics of the vegetative and floral morphology. Thus the identification of *Eriocaulaceae* mostly is connected with some difficulties for the following reasons: The preparation of the tiny flowers requires a high degree of patience and accuracy and still preparation-artefacts are common. Furthermore, intraspecific variation of the habit is quite abundant.

For an easier and more accurate identification of *Eriocaulaceae* it therefore becomes necessary to use additionally other characteristics than the traditional ones mentioned above.

It was DOUVAL-JOUVE (1875) who, after having studied leaves of Gramineae, first discussed the taxonomical significance of the leaf anatomy. Following DOUVAL-JOUVE'S idea, BROWN (1958) divided the *Gramineae* into several subfamilies pointing out differences in the leaf anatomy. His system is based on own observations and results of other authors.

The leaf anatomy of *Eriocaulaceae* has been studied by many authors (POULSEN 1888; RUHLAND 1903; TOMLINSON 1969, and others). Only recently GIULIETTI (1978), CASTRO (1986), HENSOLD (1988) and SCATENA (1990) also considered taxonomical aspects, but their contributions are limited to (sub-) genera with in some cases geographical restrictions.

2. Material and methods

2.1. Material

The *Eriocaulaceae* investigated were collected by S. SPLETT in the Federal District of Brasília, Brazil, between January and July of 1990. The plants were fixed in FAA; five individuals of each species were herbarized. Specimens of each species were deposited in the herbaria of the Botanical Institute of the Federal University of Brasília (UnB), the Botanical Garden Brasília, and the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE).

The following list gives the taxa examined; to the species cultivated in the Botanical Garden of Bonn [Bonn (BG)] the accession number is added.

Eriocaulon L.

- Eriocaulon modestum* KUNTH, Bonn (BG) 011209
- Eriocaulon sellowianum* KUNTH
- Eriocaulon* spec., Splett No. 11
- Eriocaulon* spec., Splett No. 24, Bonn (BG) 07820

Paepalanthus KUNTH

- Subgenus *Paepalocephalus*:
- Section *Actinocephalus*

Paepalanthus hilairei KOERN.

Section *Diphyomene*

- Paepalanthus acanthophyllus* RUHL.
- Paepalanthus flaccidus* (BONG.) KUNTH
- Paepalanthus speciosus* (BONG.) KOERN.

Section *Eriocaulopsis*

- Paepalanthus elongatus* (BONG.) KOERN.
- Paepalanthus scandens* RUHL.
- Paepalanthus subulatus* KLOTZSCH

Syngonanthus RUHL.

Section *Carphocephalus*

- Syngonanthus appressus* (KOERN.) RUHL., Bonn (BG) 07822
- Syngonanthus caulescens* (POIRET) RUHL.

Section *Dimorphocaulon*

- Syngonanthus densiflorus* (KOERN.) RUHL., Bonn (BG) 011213
- Syngonanthus fischerianus* (BONG.) RUHL., Bonn (BG) 07819
- Syngonanthus gracilis* (BONG.) RUHL.
- Syngonanthus helminthorrhizus* (KOERN.) RUHL.
- Syngonanthus nitens* (BONG.) RUHL.
- Syngonanthus* cf. *pulcher* (KOERN.) RUHL., Bonn (BG) 11211

Syngonanthus simplex (MIQ.) RUHL.

Syngonanthus spec. Splett No. 35

Section *Thysanocephalus*

Syngonanthus xeranthemoides (KOERN.) RUHL., Bonn (BG)
11212

2.2. Methods

As far as possible specimens of one species were collected from ecologically different habitats within a population to facilitate the separation of characters of ecological and taxonomic significance. *Syngonanthus appressus* was chosen, because this species has the

3. Observations

The species studied of *Eriocaulon* are hygrophytes with partially submerged leaves. Members of *Paepalanthus* mostly occur in dry habitats and generally show xeromorphic characters, whereas in *Syngonanthus*, some species can be found in dry, others in wet habitats.

The leaves of the *Eriocaulaceae* are linear to lanceolate or ligulate, their bases normally are slightly widened. They in general are spirally arranged forming basal rosettes. Species with leafy aerial stems (*P. flaccidus*, *P. speciosus*, *P. scandens*, *P. hilairei*, *S. appressus*, *S. caulescens*, *S. helminthorrhizus*, and *S. spec. Splett No. 35*) often present leaves with sheathing bases, which may or may not completely encircle the stem.

3.1. Anatomy of the leaves

Epidermis – The cells of the epidermis are longitudinally extended, in surface view mostly rectangular and arranged in longitudinal rows. The abaxial epidermis cells are generally differentiated into costal and intercostal bands, which is a common feature of the *Eriocaulaceae*. The anticlinal cell walls of the epidermis usually are non-sinuuous, the generally flat or slightly convex periclinal cell walls may be thin or thickened. The cuticle is smooth or inconspicuously striate (terminology sensu BARTHOLOTT 1981). The cells of the lower epidermis usually are smaller than the cells of the upper surface. However, the cells are of equal size on both surfaces in *E. spec. Splett No. 11*, *S. helminthorrhizus* and *S. xeranthemoides*, or they are adaxially smaller in *P. acanthophyllus*.

The outer epidermis walls of more xerophytic taxa (all *Paepalanthus* spp. studied, *S. densiflorus*, *S. helminthorrhizus*, *S. xeranthemoides*) normally are thickened and sclerified, whereas in hygrophytic species (*Eriocaulon*) epidermal cell walls remain thin.

basal leaves generally submerged and the upper leaves always emers. Thus an intraspecific variability due to environmental influence could be expected in a single specimen.

Freehand sections were obtained from the basal, median, and apical region of fixed leaves, in order to gain information about the different stages of differentiation of the leaf tissues. The sections were stained in phloroglucine (JOHANSEN 1940) for brightfield microscopy.

For the SEM examination, pieces of the median regions of fixed leaves were dried by the critical-point method after GERSTBERGER & LEINS (1978), changing FAA against formaldehyde dimethyl acetal, which in its turn was substituted by CO₂. Subsequently the leaves were sputtered with gold and studied in a Cambridge Stereoscan 200.

A peculiar feature of all *Paepalanthus* spp. studied is the local appearance of a seemingly biseriate epidermis, which is caused by diagonal anticlinal cell walls. Furthermore, the existence of large inwardly growing, "teethlike" (SOLE-REDER & MEYER 1929) protuberances in the abaxial epidermis is typical for the taxa investigated. The protuberances penetrate deeply (*P. hilairei*, *P. acanthophyllus*, *P. scandens*, *P. subulatus*) or less deeply (*P. elongatus*, *P. flaccidus*, *P. speciosus*) into the mesophyll. Only in *P. acanthophyllus* the protuberances are also developed in the upper epidermis.

In all *Eriocaulaceae* the stomata are of the *Gramineae*-type (see TOMLINSON 1969) and occur usually in the intercostal regions. In most species the stomata are restricted to the abaxial surface; only *E. spec. Splett No. 24*, *S. helminthorrhizus*, *S. fischerianus*, and *S. subulatus* show amphistomatic leaves. Stomata are limited to the intercostal regions, forming one to six adjacent stomatal bands in each intercostal band. The stomata may be on the same level as the other epidermal cells (*E. spec. Splett No. 11*, *P. hilairei*, *P. scandens*, *P. subulatus*, *S. densiflorus* und *S. spec. Splett No. 35*), slightly sunken in (*E. sel-lowianum*, *E. spec. Splett No. 24*, *P. acanthophyllus*, and *P. speciosus*) or raised, as in the other species observed.

Hypodermis – Some of the species investigated present a one- to pluri-layered hypodermis lining the upper (and lower) epidermis. The mostly large hypodermal cells lack chlorophyll, and may have more or less thickened or sclerified (*P. speciosus*) cell walls. Further details are given in chapter 3.2.

Mesophyll – The mesophyll of the *Eriocaulaceae* generally is differentiated into a one- to three-layered, mostly adaxially situated palisade parenchyma and a strongly developed spongy parenchyma. Only in *P. scandens*, *P. subulatus*, *S. gracilis*, *S. simplex* the palisade cells are of the typical elongated-prismatic shape. In the majority of the taxa studied the tissue consists of up to two rows of

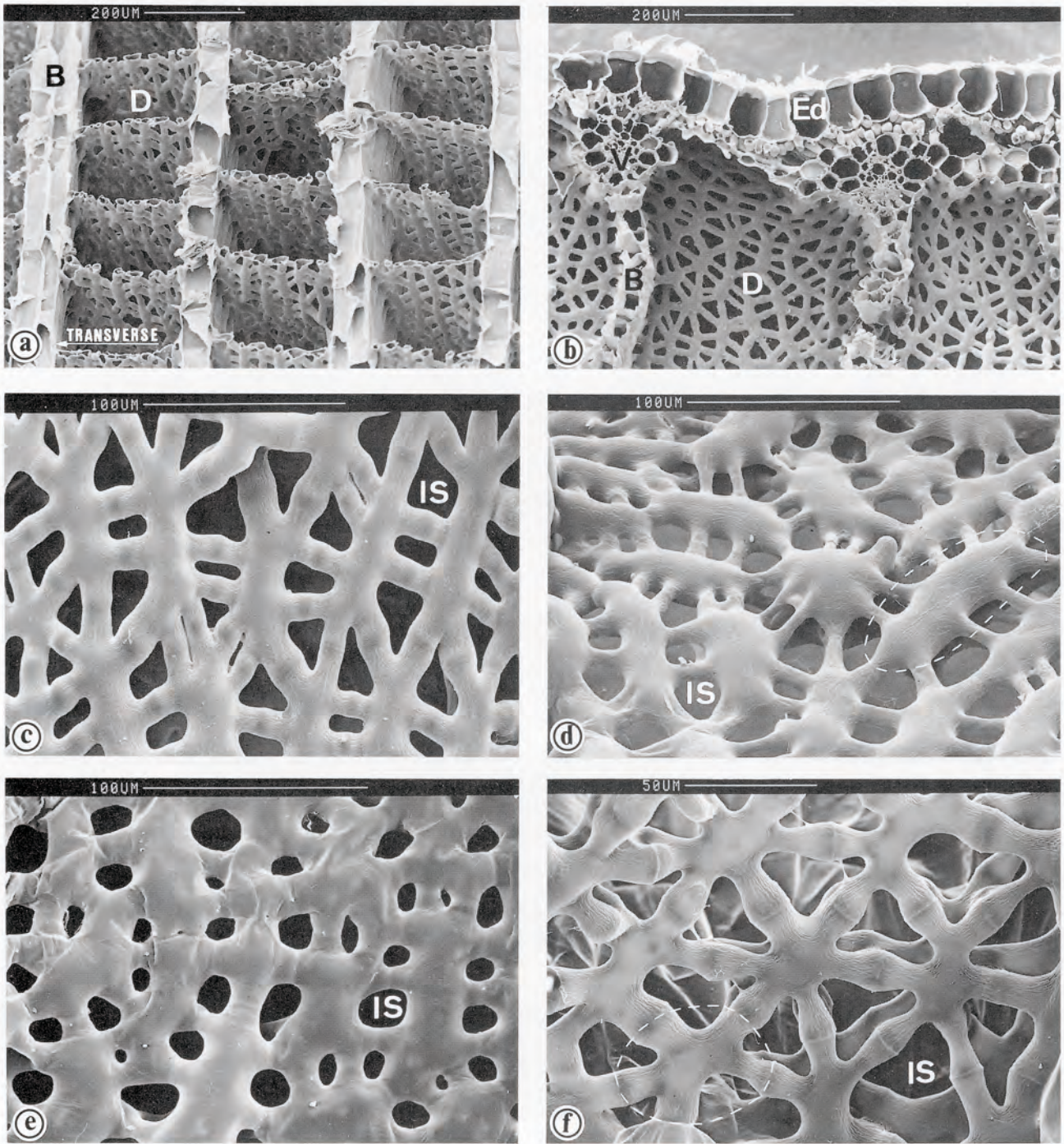


Fig. 1. SEM-micrographs of diaphragms of hygrophytic *Ericaulaceae*. a) Longitudinal section (LS), b–f) TS of leaves. a) *E. sellowianum*. View showing aerenchyma with transverse diaphragms (D) between buttresses (B). b) *E. sellowianum*. View on diaphragm (D), adaxial epidermis (Ed), buttresses (B) and vascular bundles (V). c–f) Stellate diaphragm-cells of *E. sellowianum* (c), *E. modestum* (d), *E. spec.* Splett No. 11 (e) and *S. spec.* Splett No. 35 (f). Stellate cells with longitudinally extended (c, d, e) or almost quadrangular (f) cell-body. In d) and f) one cell each has been demarcated by broken lines. Intercellular spaces = IS.

rounded or oval cells with large intercellular spaces in between. Therefore descriptions sometimes mention "palisade parenchyma lacking".

In all species investigated there is a spongy parenchyma, which may be homogeneously net-like or differentiated into a special aerenchyma, as in many hygrophytic species (*Eriocaulon* spp., *S. cf. pulcher*, *S. spec.* Splett No. 35). This aerenchyma is composed of transverse uniseriate diaphragms segmenting large lacunae at regular intervals (fig. 1 a), producing fenestrate leaves. The diaphragm-cells are of stellate shape with more or less large intercellular spaces (fig. 1 b–f), and contain chlorophyll.

The spongy parenchyma of the *Paepalanthus* ssp. and *S. xeranthemoides* is dense with small intercellular spaces, whereas it is relatively loose with large intercellular spaces in all the other *Syngonanthus* species.

According to POULSEN (1888), oxalate-crystals of different shapes can be found in the leaf-mesophyll of *Eriocaulon*, *Paepalanthus* and *Syngonanthus* spp. Of all the species studied, calciumoxalate-crystals could only be recorded in the diaphragm-cells *S. cf. pulcher*. One of the species observed (*P. elongatus*) contained amyloplasts in the mesophyll of its leaves. As TOMLINSON (1969) reports, storage of starch is quite common in the rhizoms of *Eriocaulaceae*.

Vascular bundles — The vascular bundles of the *Eriocaulaceae* are collateral without a cambium. They are surrounded by two sheaths: The inner sheath normally is one- to two-layered with thick or sclerified cell walls, whereas the outer consists of large, thin-walled parenchymatous cells. The bundle sheath lacks intercellular spaces and contains in contrast with *Poaceae* no chloroplasts.

Buttresses — Bundle-sheath extensions, or buttresses, joining the veins to the upper and/or lower epidermis are a common feature in the *Eriocaulaceae*. The cells are large and free of chlorophyll and their walls may be slightly thickened, collenchymatous (*S. densiflorus*) or sclerified (*P. acanthophyllus*, *P. speciosus*).

3.2. Typology of leaf tissue distribution patterns

The distribution of the leaf tissues has proven to be quite variable. The different types of leaf transverse sections are illustrated schematically in fig. 2. Since the level of the transverse section often is of eminent importance (TOMLINSON 1969, observations of the authors), the schemes consider transverse sections of the middle of the leaf. As the leaves of *Eriocaulaceae* show a strictly basiplast growing mode, the middle of the leaf is not per se a homologous position in all cases. But transversal sections from the middle of the leaf will normally be far enough away from the basal growing zone and show a fully differentiated

situation and will not be too close to the apex, which can show special reduced anatomical features. At the leaf bases the hypodermal and buttressing tissues generally are more developed. The veins more frequently are buttressed to both surfaces. Furthermore, the cell walls of the mechanical tissues (buttresses and inner bundle sheath) normally are thicker and more often sclerified.

Hypodermis — A well developed and continuous adaxial hypodermis is present in *E. spec.* (Splett No. 11), *P. elongatus*, *S. densiflorus*, *S. helminthorrhizus*, *S. nitens* and *S. spec.* Splett No. 35, only in *P. speciosus* it is discontinuous. In *S. xeranthemoides* the hypodermal layer is continuous and multiseriate on both sides. In the other species investigated the hypodermis is absent.

Mesophyll — In most species the palisade parenchyma is situated below the adaxial epidermis or hypodermis; in *E. spec.* Splett No. 11, *E. sellowianum*, *P. subulatus*, *S. appressus* (emersed leaves), and *S. pulcher* it also is lining the lower epidermis or hypodermis. It may be continuous or discontinuous being interrupted by buttresses (*E. spec.* Splett No. 11, *S. densiflorus*, *P. speciosus*, *P. flaccidus*, emerse leaves of *S. appressus*, and *S. cf. pulcher*). In *P. subulatus* a kind of palisade parenchyma can be found in radial orientation around the vascular bundles. The palisade parenchyma evidently is lacking in *P. acanthophyllus*, *P. elongatus*, *P. hilairei*, *S. helminthorrhizus*, and *S. xeranthemoides*.

Vascular bundles — The vascular bundles usually are arranged in a single series. They can be more or less equidistant from each surface (*E. spec.* Splett No. 11, *E. spec.* Splett No. 24, *P. acanthophyllus*, *P. elongatus*, *P. hilairei*, *P. scandens*, *P. speciosus*, *P. subulatus*, *S. densiflorus*, *S. helminthorrhizus* and *S. cf. pulcher*) or closer to the adaxial (*E. modestum*, *E. sellowianum*, *P. flaccidus*, *S. appressus*, *S. caulescens*, *S. fischerianus*, *S. gracilis*, *S. simplex*, and *S. spec.* Splett No. 35) or abaxial (*S. nitens*, *S. xeranthemoides*) epidermis. Usually two or three orders of size are evident, generally one large vein alternating with one to three smaller veins. The size of the veins is decreasing from the middle to the margin of the leaves, as in most monocotyledons.

Buttresses — In the majority of the species with veins closer to the adaxial epidermis, buttresses joining the veins to the abaxial surface are observed (*E. modestum*, *E. sellowianum*, *S. fischerianus*, *S. gracilis*, *S. simplex*, and *S. spec.* Splett No. 35). In the other species the major veins are buttressed to both surfaces and the minor veins only to the adaxial (*E. spec.* Splett No. 24, *P. acanthophyllus*, *P. elongatus*, *P. hilairei*, *S. caulescens*, *S. nitens*, *S. pulcher*, and *S. xeranthemoides*) or the abaxial (*S. helminthorrhizus*) epidermis/hypodermis, if at all. In *S. helminthorrhizus* the adaxial buttresses are reduced to small caps covering the veins. In general the buttresses do not connect adjacent veins. Exceptions are given in *S. densiflorus* (only leaf base) and *S. helminthorrhizus*.

Table 1. Useful characters and character states from fig. 2.

1. hypodermis
 - a) present on both sides (k)
 - b) present only on adaxial side (b, d, f)
 - c) lacking (a, c, e, g, i)
2. palisade parenchyma
 - a) lacking on both sides (a, b, h, k)
 - b) present only on adaxial side (c, g, d, f)
 - c) present on both sides (e, i)
 - d) in radial orientation around the vascular bundles (j)
3. palisade parenchyma on adaxial side
 - a) interrupted by buttresses of vascular bundles (e, f, i)
 - b) forming a continuous layer (c, d, g)
4. palisade parenchyma on abaxial side
 - a) interrupted by buttresses of vascular bundles (e)
 - b) forming a continuous layer (i)
5. vascular bundles
 - a) more or less in the middle of the mesophyll (e)
 - b) closer to the adaxial epidermis (a, b)
 - c) closely attached to the adaxial palisade parenchyma (c, d)
 - d) closer to the abaxial epidermis (h)
6. vascular bundles
 - a) all more or less of the same size (c, g, i, k)
 - b) of different size (b, f)
7. small and large bundles
 - a) alternating regularly (b)
 - b) alternating irregularly (f)
8. buttresses (attachment of vascular bundles)
 - a) joining all bundles to both surfaces
 - b) joining only the main bundles to both sides and the others to one side (a, e, k)
 - c) joining only the main bundles to both sides and the others without attachment (f)
 - d) joining all bundles only to one side (c, d, h)
 - e) lacking at all (g)
9. unilaterally attached bundles (attachment)
 - a) attached only to the adaxial side (a, b, i)
 - b) attached only to the abaxial side (c, d, h, k)
 - c) attached to the abaxial or to the abaxial side (e)
10. buttress "cap" on the other side of unilaterally attached bundles
 - a) bundles
 - b) present (h)
 - c) absent
11. buttresses
 - a) connecting adjacent bundles
 - b) not connecting adjacent bundles

The matrix is designed for descriptive purposes. Character states which have never been reported are omitted. For cladistic use, at least some of the characters have to be broken into two or more characters (e.g. 2 and 8).

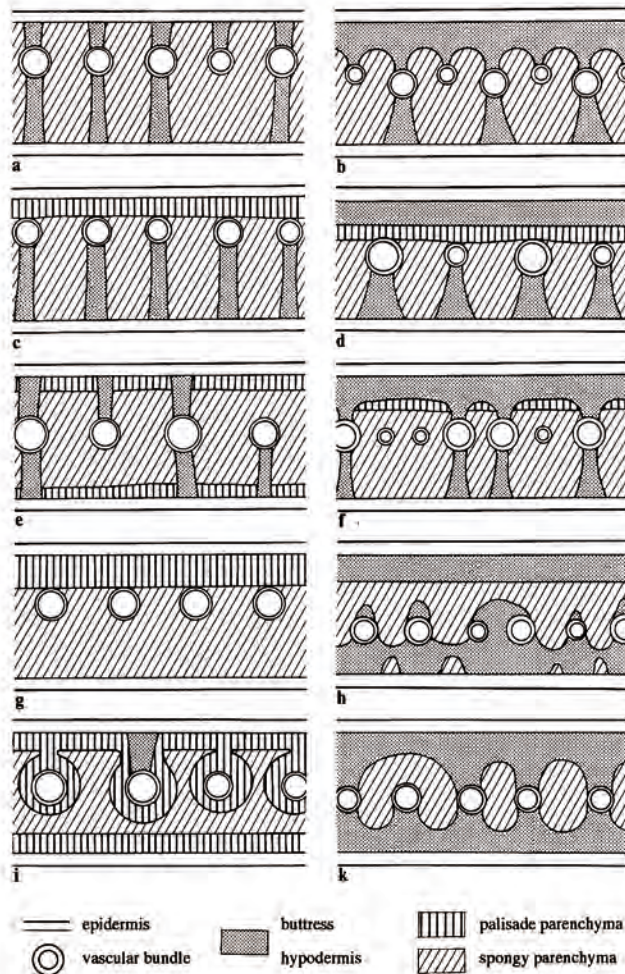


Fig. 2. Distribution of leaf tissues in *Eriocaulaceae*. Diagrammatic transverse section (TS). a) *P. acanthophyllus*, *P. flaccidus* (smaller vascular bundles (VBs) only buttressed to abaxial epidermis), *P. hilairei*. b) *P. elongatus*. c) *E. modestum*, *S. appressus* (submerged leaves), *S. fischerianus*, *S. gracilis*, *S. simplex*. d) *S. nitens*. e) *E. spec.* Splett No. 11, *E. spec.* Splett No. 24, *S. appressus* (emersed leaves), *S. cf. pulcher*. f) *P. speciosus*, *S. densiflorus*, *S. spec.* Splett No. 35 (all VBs buttressed to adaxial epidermis). g) *P. scandens* (median VB in some plants buttressed to both epidermises), *S. caulescens* (median VB in some plants buttressed to adaxial epidermis). h) *S. helminthorrhizus*. i) *P. xeranthemoides*.

3.3. Typology and distribution of trichomes

Hairs are present in the adaxial and/or abaxial epidermis of all *Eriocaulaceae* investigated. The distribution of the trichomes and their types are listed up for each species in table 2. The trichomes are always uniseriate and regularly consist of a basal, a collar and at least one filamentous cell. The basal cell, resulting from inequal division of an epidermal cell, mostly is wedged into the epidermis, and usually is smaller than a normal epidermis cell. It may be rounded, rectangular, almost quadrangular or protruding bulbous (fig. 3; VII). The collar cell in general is flat, it's walls often cutinized and yellowish-brown. The walls of the filamentous cell(s) commonly are smooth, in some cases undulating (fig. 3; V) or spinulose (fig. 3; X). The distal end of the apical filamentous cell normally is acute (fig. 3; I, II, IV), sometimes oblique (fig. 3; V) or rounded (fig. 3; II). The distal cells may be unbranched or two-branched as in the T-shaped Malpighian-hairs (fig. 3; VIII–X). The two branches in general are orientated longitudinally (e.g. parallel to the epidermal cells). The shape of Malpighian-hairs is varying from symmetric to totally asymmetric. Usually the collar cell is absent in the Malpighian-hairs. Glandular hairs (fig. 3; VII) occur in *S. helminthorrhizus* in large number on both sides of the leaves and sporadically in the abaxial epidermis of *S. appressus*.

Table 2. Distribution of hairs on leaves of *Eriocaulaceae*. The numbers mentioned below are referring to the hair types presented in fig. 3.

species	adaxial leaf surface	abaxial leaf surface	leaf-margin
<i>Eriocaulon</i>			
<i>E. modestum</i>	III	III	
<i>E. sellowianum</i>	III	III	
<i>E. spec. Splett No. 11</i>	III	III	
<i>E. spec. Splett No. 24</i>	I	I	
<i>Paepalanthus</i>			
Section <i>Actinocephalus</i>			
<i>P. hilairei</i>	I	I	II
Section <i>Diphyomene</i>			
<i>P. acanthophyllus</i>	I		II
<i>P. flaccidus</i>		IX	II
<i>P. speciosus</i>			I
Section <i>Ericaulopsis</i>			
<i>P. elongatus</i>	I	I	I
<i>P. scandens</i>	II	II	V
<i>P. subulatus</i>	IX	IX	IX
<i>Syngonanthus</i>			
Section <i>Carphocephalus</i>			
<i>S. appressus</i>	I, VII, X	I, VIII, X	X
–, submerged leaves	I, X	I, VIII, X	X
<i>S. caulescens</i>	X	X	X
Section <i>Dimorphocaulon</i>			
<i>S. densiflorus</i>	IX	IX	I
<i>S. fischerianus</i>	X	X	X
<i>S. helminthorrhizus</i>	I, VII	I, VII	I
<i>S. nitens</i>	I, IX	IX	
<i>S. cf. pulcher</i>	I, IX	I, IX	I
<i>S. simplex</i>	I, IV	X	
<i>S. spec. Splett No. 35</i>	X	X	
Section <i>Thysanocephalus</i>			
<i>S. xeranthemoides</i>	IX	IX	

4. Discussion

4.1. Variability of leaf anatomy

Since the habit of some *Eriocaulaceae* may be highly variable, it is always very important to collect as many plants with different habitus of a single population as possible. So it is possible to separate variable and constant characters without running the risk of mixing up specimens from different species or dealing different forms of same species as different taxa, both errors which are not uncommon in *Eriocaulaceae*. As one example of extreme variability *S. caulescens* may be mentioned. This species produces acaulescent individuals or plants with stems up to 30 cm high as well as all intermediate forms. All individuals can be identified as *S. caulescens* because of other

constant characters, such as phyllotaxis, organization of the inflorescences, shape of the capitulum and floral morphology. The investigation of many different plants of one taxon has shown, that arrangement and structure of the different tissues are fairly consistent characters on species level, whereas the number of veins varies depending on the width of the leaves.

4.2. Taxonomic significance of the leaf anatomy

Epidermis – Having investigated the leaves of graminees PRAT (1932) concluded that the shape of epidermis- and stomata-cells as well as the pubescence of vegetative

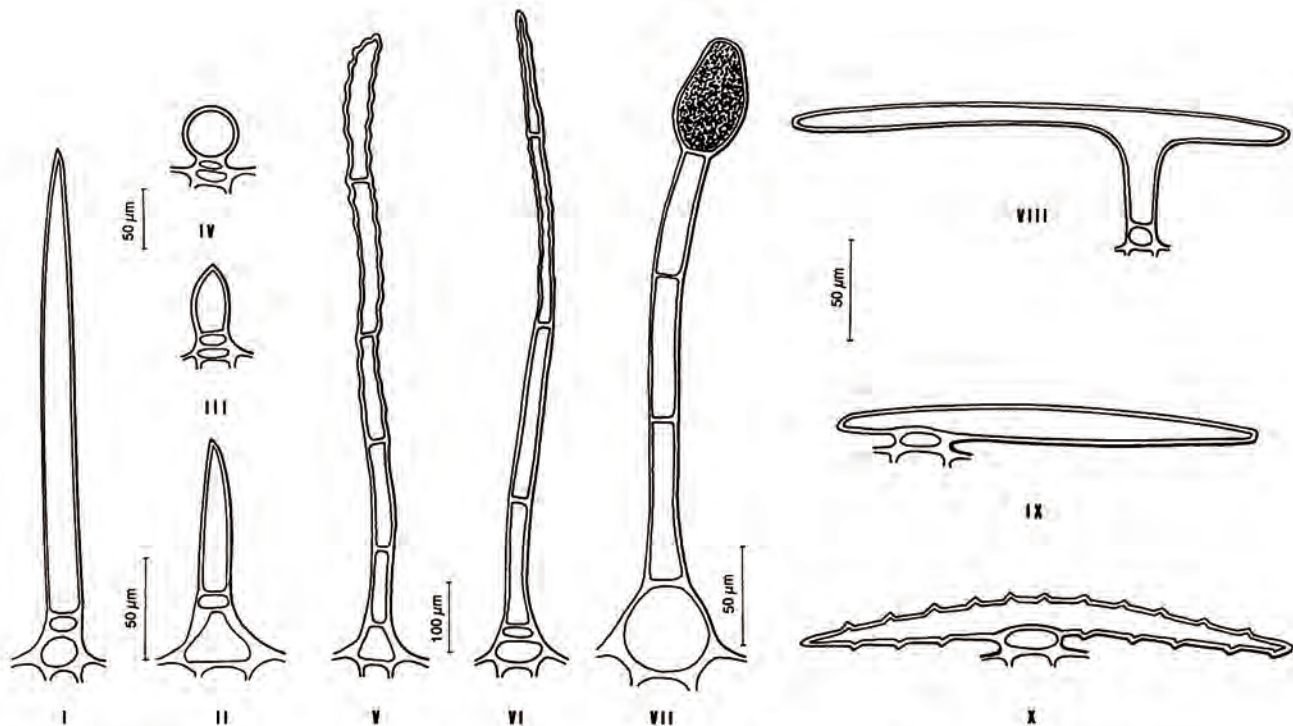


Fig. 3. Hair types on leaves of *Eriocaulaceae*. I–VI) Filamentous hairs. VII) Glandular hair. VIII–X) Malpighian-hairs.

organs are genera-specific features, the dimension of the cells mentioned above even being consistent characters of varieties. As our results and investigations made by other investigators (CASTRO 1986; HENSOLD 1988; MONTEIRO et al. 1984; POULSEN 1888; RUHLAND 1903; SCATENA 1990; TOMLINSON 1969) indicate, in *Eriocaulaceae* the epidermis features do not correlate with (sub-) generic boundaries as clearly as in the *Gramineae*.

Own results conform to the data obtained by HOLM (1901), MONTEIRO et al. (1984), POULSEN 1888), and TOMLINSON (1969); hygrophytic or aquatic *Eriocaulaceae* always show large, thin-walled epidermis cells, which are typical features of plants growing in humid or wet habitats.

The epidermis of *Paepalanthus* and *Syngonanthus* species is differently structured. The predominantly small cells of the more xerophytic species of *Paepalanthus* subgenus *Paepalocephalus* mostly possess thickened or sclerified cell walls, thus being well adapted to the periodically dry habitats, in which they occur.

Another consistent characteristic of the *Paepalanthus* species investigated is the locally apparently biseriate epidermis, caused by the diagonal position of the anticlinal epidermal walls. As mentioned above, the intercostal epidermis cells develop protuberances, which deeply penetrate into the mesophyll. EBEL (1885) was the first to describe this remarkable feature for the *Eriocaulaceae*, interpreting it as having mechanical function. GIULIETTI (1978) and MONTEIRO et al. (1985) name these epidermal

cells “bulliform cells”, referring to the thin walled joint cells of the *Gramineae* described by DOUVAL-JOUVE (1870). Pointing to the thickness of these epidermal walls CASTRO & MENEZES (1990) rejected the joint function of the cells in question and called them “inverted T”-cells instead, due to their T-shape. In their opinion the inverted T-cells serve for waterstorage and stabilization of the substomatal chamber.

In most species the occurrence of inverted T-cells is restricted to the abaxial epidermis. If present on both surfaces the protuberances are much longer in the lower epidermis. Length and number of the protuberances of each cell are variable within the sections but obviously consistent within species.

Inverted T-cells are absent in the subgenus *Xeractis* (HENSOLD 1988), and have not been observed in the subgenera *Platycaulon* and *Thelxinoë* (CASTRO 1986). All species presenting inverted T-cells belong to the *Paepalocephalus* sections *Actinocephalus*, *Eriocaulopsis*, and *Diphyomene* (CASTRO 1986; POULSEN 1888; SOLEREDER & MEYER 1929; TOMLINSON 1969). It seems that all species of *Actinocephalus* and *Diphyomene* show these T-cells, but obviously not all species in *Eriocaulopsis* do so. The T-cells are not clearly correlated with ecological factors (there are species without T-cells in the same habitats), but in two well defined groups (*Actinocephalus* and *Diphyomene*) an obvious correlation to the taxonomy is visible. Therefore it makes sense to analyse this character can be

used to break *Eriocaulopsis* into natural units and to find the sister groups for these units. The results indicate that T-cells are typical features of the *Paepalocephalus*-sections mentioned above. Similar epidermis cells were found in some species of the genus *Leiothrix* (GIULIETTI 1979; MONTEIRO et al. 1985).

Within *Syngonanthus*, the appearance of the epidermis is quite variable. A common feature of the sections *Dimorphocaulon* and *Carphocephalus* are large, thin-walled epidermal cells. Within these sections only *S. densiflorus* and *S. helminthorrhizus* present small and sclerified epidermal cells. Similarly structured are *S. xeranthemoides* and other *Thysanocephalus*-species, studied by SCATENA (1990) and STÜTZEL & BRIECHLE (1990). This is one more example for the taxonomic value of anatomical features. On the other hand it is not of much practical use in this case, as *Thysanocephalus* is characterised by several morphological characters and the two sections *Dimorphocaulon* and *Carphocephalus*, which are in some cases difficult to distinguish, show no marked differences in leaf anatomy.

The evaluation of all data available indicate a certain taxonomic applicability of the epidermal features on generic level. In some cases the epidermis anatomy can facilitate the identification of species. As example may be mentioned *S. densiflorus* with in surface view short but broad epidermis cells and *S. xeranthemoides*, which possesses small cells with thickened and yellowish walls. *P. speciosus* and, according to SCATENA (1990), some species in other subgenera produce epidermis cells with sclerified and irregularly thickened cell walls on both surfaces. The thickenings are strongest in the median region of the outer pericline cell wall. Collaps of the cell walls can be excluded as a cause of this epidermal structure since the cell walls are sclerified. SCATENA (1990), studying *P. speciosus*, did not observe these local wall thickenings of the epidermis cells. However, considering the great number of varieties within this *P. speciosus*, it is possible that two different varieties were investigated, each with typical features.

Hypodermis – Emphasizing obvious anatomical similarities between the hypodermis and the vein buttresses, TOMLINSON (1969) interpreted the hypodermis as being a lateral extension of the buttresses. Ontogenetical studies about origin and development of the hypodermal layer so far have not been made in the *Eriocaulaceae*. The function of the buttresses is supposed to be stabilization of the leaves (ESAU 1965; HENSOLD 1988).

As to the systematical applicability of the distribution of the hypodermis no correlations on (sub)generic level are visible. One exception is the *Syngonanthus*-section *Thysanocephalus* with quite uniform leaf anatomy (SCATENA 1990; own observations).

Vascular bundles – Within the *Gramineae* a correlation between the ultrastructure of the outer, parenchym-

atous sheath and the division into subgenera apud BROWN (1958) was observed (CAROLIN et al. 1973). In agreement with results presented by CASTRO (1986), HENSOLD (1988), SCATENA (1990) and TOMLINSON (1969) our investigations do not show such a clear connection between the anatomy of the bundle sheaths and the division into subfamilies and/or genera. However, some tendencies within the genera are visible: In *Paepalanthus* the cells of the outer bundle sheath are almost equal in size, whereas the size of the cells is variable in *Eriocaulon* and *Syngonanthus*. Unlike in *Eriocaulon*, the cells of the outer bundle-sheath are clearly different from the buttress-cells in *Paepalanthus* and *Syngonanthus*.

The inner bundle-sheath shows some adaptations to habitat-conditions: in xeromorph leaves the cell walls are thickened and sclerified from the leaf base to the apex, whereas in hygrophytic species this is only the case at the leaf base. The sclerification is a late process in the ontogeny. If it occurs only at the base of a basiplast leaf, the lack of sclerification in the distal part of the leaf can not be an effect of an earlier stage of differentiation in this part. In some species, as in *E. septangulare* WITH. (HOLM 1901), *E. spec.* Splett No. 11, *S. fischerianus*, *S. nitens*, *S. spec.* Splett No. 35, and *S. xeranthemoides*, yellow or orange cell walls are a consistent character.

Anastomoses between the longitudinal bundles by lateral bundles have been reported as occurring regularly in the aerenchyma of monocotyledoneous waterplants, and being very rare in dicotyledonous hydrophytes (DOUVAL-JOUVE 1873). According to POULSEN (1888) and RUHLAND (1903) anastomoses are always absent in *Eriocaulaceae*. Refuting this statement many following investigations indicate that lateral veins are a common but not consistent feature of hygrophytic or aquatic *Eriocaulaceae*. Anastomoses were found in all *Eriocaulon* spp. studied, in *S. xeranthemoides* and, according to HOLM (1901) and TOMLINSON (1969), in some other *Eriocaulon*-species. So far anastomoses could be observed in only two xerophytic species (*S. cipoensis* RUHL. and *S. rufipes* SILVEIRA). Considering their function, the presence of lateral veins mainly in hygrophytic plants seems quite questionable. The frequent occurrence of anastomoses should rather be expected in xerophytic plants in order to gain a more efficient transport of water. Anastomosing lateral bundles have a bundle sheath, but no buttresses, which attach the bundles to the epidermis, and therefore are not translucent from the surface. As there are not so many lateral bundles, they often do not appear in transverse sections. In spite of repeated studies of longitudinal sections of the more xerophytic species (all *Paepalanthus* spp., *S. densiflorus*, *S. helminthorrhizus*) no anastomoses were found.

Palisade parenchyma – As mentioned before, the structure of the palisade parenchyma – if present at all – is quite variable. Our results confirm the conclusions by CASTRO (1986) and SCATENA (1990) according to which

the palisade parenchyma is always absent in the *Paepalanthus*-sections *Actinocephalus* and *Diphyomene* and in the *Syngonanthus*-section *Thysanocephalus*.

Notable is an observation, which has been reported previously by HARE (1950) and MONTEIRO et al. (1984): In *Eriocaulaceae* with (periodically) submerged leaves the palisade parenchyma forms a continuous one- or two-seriate layer, while in xerophytic species, the palisade parenchyma is generally interrupted by the buttresses. As assumed by MONTEIRO et al. (1984) this arrangement is due to the lack of light under water, which in parts is compensated by a high number of chlorophyll-rich cells. Our results strengthen the assumption of this feature being a result of an adaptation to certain ecological conditions: *S. appressus* bears emergent as well as submerged leaves which are sharply anatomically differentiated (fig. 1c, e).

Diaphragms — Large air-lacunae, segmented by transverse, uniseriate diaphragms are a common feature in monocotyledoneous waterplants (NAPP-ZINN 1973; KAUL 1971, 1972; SNOW 1914; TOMLINSON 1969, and others). GUETTARD (1747) was the first to mention diaphragms in the aerenchyma of water plants (NAPP-ZINN 1973). Within the *Eriocaulaceae* aerenchyma occur in leaves of many species of *Eriocaulon* (ARBER 1922; HOLM 1901; KOERNICKE 1863; MONTEIRO et al. 1984; POULSEN 1888; RUHLAND 1903; SOLEREDER & MEYER 1929; TOMLINSON 1969). The aerenchymatic tissue in roots of *Eriocaulaceae* clearly is different in histology and histogeny from the aerenchyma of the leaves and was described, also under the systematical and ecological aspects, by STÜTZEL (1988). In our investigation the structure of the aerenchyma was analysed from the taxonomical point of view. The results lead to the assumption that the shape of the stellate cells may be helpful for the identification of species: The cellbody may be elongated (fig. 2c, d, e) or almost quadrangular (fig. 2f). Analysing other features of the diaphragm-cells (length of the lobes, size of the intercellular spaces between the lobes) one always has to consider that the intercellular spaces become larger during histogeny and are therefore smaller at the leaf base.

The organization of the leaf tissues was found to be consistent within species but showing a high degree of variability on (sub-) generic level (CASTRO 1986; HARE 1950; HENSOLD 1988; HOLM 1901; MONTEIRO et al. 1984; SCATENA 1990; TOMLINSON 1969; own results). Thus in many cases it has not proven to be a valuable feature for the distinction between sections and genera. As one of the exceptions the *Syngonanthus*-section *Thysanocephalus* can be mentioned. According to SCATENA (1990) the leaf anatomy of the *Thysanocephalus*-species is very uniform and coincides with our studies of *S. xeranthemoides*, the *Thysanocephalus* spp. studied by the authors.

Despite of the high degree of variability mentioned above, the distribution of the leaf tissues to some extent seems to be adapted to ecological conditions:

Typical features of periodically submerged leaves evidently are adaxially situated vascular bundles, which are buttressed to the abaxial epidermis. The palisade parenchyma is a continuous layer composed of rounded to oval cells.

The leaves of hygrophytic or more xerophytic species normally present vascular bundles equidistant to both surfaces. The buttresses mostly are joining the major veins to the adaxial and abaxial epidermis/hypodermis. The hypodermis which is developed in hygromorph leaves generally as a discontinuous one- to two-seriate layer, is often lacking in xerophytic species.

Trichomes — TATEOKA et al. (1959) found, that *Gramineae*-subfamilies as well as some of the genera show typically structured bicellular microhairs. With certain restrictions this result can be transferred to the tree *Eriocaulaceae*-genera studied.

In *Eriocaulaceae* studies on hairs have been quite scarce and mostly limited to anatomical descriptions (POULSEN 1888; HOLM 1901; SOLEREDER & MEYER 1929; HARE 1950; TOMLINSON 1969). STÜTZEL & BRIECHLE (1990) investigated water-absorptive hairs in *Eriocaulaceae*. The usefulness of floral trichome characters in the taxonomy of the *Eriocaulaceae* has first been pointed out by KOERNICKE (1863) and later by RUHLAND (1903). In an investigation of hairs on reproductive organs in the *Eriocaulaceae*, MONTEIRO et al. (1979) observed the structure of trichomes having diagnostic significance on generic and sectional level, sometimes serving to differentiate closely related species. HENSOLD (1988), in her morphological and systematic treatment of the *Paepalanthus* subgenus *Xeractis*, discussed the taxonomic value of the diameter and shape of the apical cell of floral trichomes, concluding that it might be especially useful to distinguish related species. MALMANCHE (1919), having investigated the anatomy of vegetative organs of *Eriocaulaceae*, pointed to the species-specific size and shape of the glandular hairs on the scapes (MONTEIRO et al. 1979) and stressed the distribution of hairs on leaves as a diagnostic feature (TOMLINSON 1969). Finally, the shape and size of hairs on leaves may have a certain taxonomic value according to TOMLINSON (1969).

In the species investigated the occurrence of trichomes in intercostal bands is a species-consistent but not section-typical characteristic.

All data available so far imply *Eriocaulon* being characterized by three- to four-celled filamentous, hyaline hairs, scattered on both surfaces. Some species are glabrous or nearly glabrous, but in many species the indumentum gets lost on old parts of the plant. The apical cells may be rounded (*E. modestum*), oval (*E.*

sellowianum, *E. spec.* Splett No. 11) or oblong (*E. spec.* Splett No. 24).

In the *Paepalanthus* species investigated pluricellular filamentous trichomes with smooth, rarely undulated (*P. scandens*) cell-walls are the most abundant hair-type. Unlike in *Eriocaulon* these hairs often possess more than two filamentous cells (*P. acanthophyllus*, *P. elongatus*, *P. flaccidus*, *P. hilairi*) and the basal call can be protruding bulbous in some species (*P. acanthophyllus*, *P. flaccidus*, *P. hilairi*, *P. scandens*). Generally the hairs are present on both surfaces, in the *Syngonanthus*-section *Diphyomene* they are restricted to the adaxial (*P. acanthophyllus*) or abaxial (*P. flaccidus*) epidermis. Contrary to observations of CASTRO & MENEZES (1990) the pubescence of *P. speciosus* was found to be only marginal. As mentioned earlier, differing results in this species may be caused by the unsettled taxonomy of the *P. speciosus* complex, so that different varieties or even different species have been studied.

Malpighian-hairs seem to be very rare in *Paepalanthus* (they were only found in *P. flaccidus* and *P. subulatus*), and have always smooth cell walls. In *Syngonanthus* Malpighian-hairs are very common, being present on both surfaces of all species studied within this genus, with the exception of *S. helminthorrhizus*. Malpighian-hairs with equally and unequally long branches may occur on the same leaf, the asymmetrical hairs mostly being restricted

5. Conclusions

Some features, as the structure of the epidermis and the vascular bundles as well as the morphology of the trichomes, generally correlate with generic boundaries. Others have proven to be helpful to distinguish sections within the genera *Paepalanthus* and *Syngonanthus*. The majority of the leaf characters are typical for a species: The distribution of the trichomes, the colour of the cell walls of the inner bundle sheath, the shape of the cellbody of the stellate diaphragm cells, and above all the distribu-

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to the leaf base and the longer branch being orientated towards the leaf apex. Some species show in addition filamentous hairs either on the leaf-margins (*P. flaccidus*, *S. densiflorus*) or scattered on the adaxial surface (*S. nitens*, *S. simplex*) or on both surfaces (*S. appressus*, *S. cf. pulcher*). Their cell walls can be smooth or, more often, spinulate or warty. Malpighian-hairs do not occur in *Eriocaulon*. Further studies should reveal if species of *Paepalanthus* with Malpighian-hairs form a natural group and if there is a closer relationship of such a group to *Syngonanthus*.

Since the hairs can get lost during the growing period of the leaf the practical taxonomic value of the trichome morphology is limited.

Similar to observations by TOMLINSON (1969) the density of the pubescence was not consistent within the species. FAHN (1967) studied the indumentum of the same species from different habitats and found, that xeromorphic plant are more pubescent than mesomorphic plants. To some extent, our results are in line with this, but it must be mentioned, that we tried to use the variability within populations to avoid taxonomical problems. Therefore, only a part of our material allows the evaluation of the question envisaged by FAHN, and additional studies with clearly defined taxa from different habitats are necessary in this respect.

tion of the tissues in many cases serve well to separate closely related species, if used in addition to vegetative and floral morphology. The leaf anatomy therefore supplies useful data for floristic work such as key making and diagnosing terminal taxa. Leaf anatomy is on the other hand also an important tool to detect phylogenetic relations up to the generic level. Some of the most useful characters with their different states are presented in table 1 and also are illustrated (fig. 1).

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References

- ARBER, A. (1922): Leaves of the *Farinosae*. Bot. Gaz. **74**: 80–94.
- BARTHLOTT, W. (1981): Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. Nord. J. Bot. **1**: 345–355.
- BROWN, W. V. (1958): Leaf anatomy in grass systematics. Bot. Gaz. **119**: 170–178.
- CAROLIN, R. C., JACOBS, S. W. L., & VESK, M. (1973): The structure of the cells of the mesophyll and parenchymatous bundle sheath of the *Gramineae*. Bot. J. Linn. Soc. **66**: 259–275.
- CASTRO, N. M. DE (1986): Estudos morfológicos dos órgãos vegetativos de espécies de *Paepalanthus* KUNTH (*Eriocaulaceae*) da Serra do Cipó (Minas Gerais). M. Sc. Thesis, unpublished, São Paulo, Brazil.
- & MENEZES, N. L. DE (1990): Considerações sobre a natureza das células altas da epiderme abaxial das folhas de *Paepalanthus* KUNTH — *Eriocaulaceae*. Bolm. Botânica, Univ. S. Paulo **12**: 95–100.
- DOUVAL-JOUVE, J. (1870): Étude anatomique de quelques Graminées. Bull. Soc. bot. France **16**: 404–410.
- (1873): Diaphragmes vasculifères des Monocotylédons aquatiques. Mém. Acad. Sci. Lett. Montpellier Sect. Sci. **8**: 157–176.
- (1875): Histoire des feuilles de Graminées. Ann. Sci. nat. 6c Sér. Bot. **1**: 294–371.
- EBEL, G. (1885): Report on observations made by G. EBEL, on the occasion of the 58th meeting of german naturalists and physicians. Bot. Centralblatt **24**: 287.
- EICHLER, A. (1875): Blüthendiagramme. Vol. 2. Engelmann, Leipzig, 136–138.
- ESAU, K. (1969): Pflanzenanatomie. Gustav Fischer Verlag, Stuttgart.
- FAHN, A. (1969): Plant anatomy. Pergamon Press, Oxford.
- (1986): Structural and functional properties of xeromorphic leaves. Ann. Bot. **57**: 631–637.
- GERSTBERGER, P., & LEINS, P. (1978): Rasterelektronenmikroskopische Untersuchungen an Blütenknospen von *Physalis philadelphia* (*Solanaceae*). Ber. Dt. Bot. Ges. **91**: 381–387.
- GIULIETTI, A. M. (1978): Modificações taxonômicas no gênero *Eriocaulon* L. Bolm. Botânica, Univ. S. Paulo **6**: 39–47.
- (1984): Estudos taxonômicos no gênero *Leiostrix* RUHL. (*Eriocaulaceae*). Tese de Livre Docência, unpublished, São Paulo, Brazil.
- (1987): Novas espécies no gênero *Leiostrix* RUHL. (*Eriocaulaceae*) para o Brasil. Bolm. Botânica, Univ. S. Paulo **10**: 15–24.
- HARE, L. C. (1950): The structure and development of *Eriocaulon septangulare* WITH. J. Linn. Soc. (Bot.) **53**: 422–448.
- HENSOLD, N. (1988): Morphology and systematics of *Paepalanthus* subgenus *Xeractis* (*Eriocaulaceae*). Syst. Bot. Monogr. **23**.
- & A. M. GIULIETTI (1991): Revision and redefinition of the Genus *Rondonanthus* HERZOG (*Eriocaulaceae*) Ann. Missouri Bot. Gard. **78**: 441–459.
- HERZOG, TH. (1924): Neue südamerikanische *Eriocaulaceae*. Feddes Repert. **20**: 82–88.
- (1931 a): Sammlung von v. Lützelburg. Feddes Repert. **29**: 82–88.
- (1931 b): Neue und weniger bekannte Eriocaulaceen aus Nordbrasilien und dem angrenzenden Venezuela. Feddes Repert. **29**: 202–213.
- HESS, H. (1955): Zur Kenntnis der Eriocaulaceen von Angola und dem unteren belgischen Kongo. Ber. Schweiz. Bot. Ges. **65**: 115–204.
- (1957): Afrikanische Eriocaulaceen. Ber. Schweiz. Bot. Ges. **67**: 83–90.
- HOLM, T. (1901): *Eriocaulon decangulare* L. an anatomical study. Bot. Gaz. **31**: 17–37.
- JOHANSEN, D. A. (1940): Plant microtechnique. McGraw Hill, New York.
- KAUL, R. B. (1971): Diaphragms and aerenchyma in *Scirpus validus*. Amer. J. Bot. **58**: 808–816.
- (1972): Adaptive leaf architecture in emergent and floating *Sparganium*. Amer. J. Bot. **59**: 270–278.
- KOERNICKE, F. (1863): *Eriocaulaceae*. In: MARTIUS, C. F. PH. VON: Flora Brasiliensis. Vol. 3, part 1. München.
- KRAL, R. (1989): The genera of *Eriocaulaceae* in the United States. J. Arnold Arb. Mass. **70**: 131–142.
- MALMANCHE, L. A. (1919): Contribution à l'étude anatomique des Eriocaulonacées et des familles voisines: Restiacées, Centrolepidacées, Xyridacées, Philhydracées, Mayacacées. Thesis, St. Cloud.
- MOLDENKE, H. N. (1949): The known geographic distribution of the members of the *Eriocaulaceae*. Suppl. 4. Phytologia **3**: 79–80.
- (1977): Additional notes on the *Eriocaulaceae* LXVII. Phytologia **35**: 252–264.
- (1982): Notes on new and noteworthy plants CLXI. Phytologia **51**: 302.
- & SMITH, L. B. (1976): Eriocaulaceae. In: REITZ, P. R.: Flora ilustrada catarinense, Itajaí, S. Catarina, Brazil.
- MONTEIRO, W. R., GIULIETTI, A. M., MAZZONI, S. C., & MORAES CASTRO, M. DE (1979): Hairs on reproductive organs of some *Eriocaulaceae* and their taxonomic significance. Bol. Botânica, Univ. S. Paulo **7**: 43–59.
- & MORAES CASTRO, M. DE (1984): Aspects of leaf structure of some species of *Eriocaulon* L. (*Eriocaulaceae*) from Serra do Cipó (Minas Gerais, Brazil). Rvta. brasil. Bot. **7** (2): 137–147.
- MORAES CASTRO, M. DE, & GIULIETTI, A. M. (1985): Aspects of leaf structure of some species of *Leiostrix* RUHL. (*Eriocaulaceae*) from the Serra do Cipó (Minas Gerais, Brazil). Revta. bras. Bot. **8**: 109–125.
- NAPP-ZINN, K. (1973): Anatomie des Blattes II. In: ZIMMERMANN, W., CARLQUIST, S., OZENDA, P., & WULFF, H. D. (eds.): Handbuch der Pflanzenanatomie. Vol. 8, part 2. A. Gebrüder Bornträger, Berlin, Stuttgart.
- PRAT, H. (1932): L'épiderme des Graminées. — Etude anatomique e systematique. Ann. Sci. nat. bot. Sér. 10, **14**: 117–325.
- POULSEN, V. A. (1888): Anatomiske Studier over Eriocaulaceerne. Vidensk. Medd. naturh. Foren. ser 4, **10**: 221–385.

- RUHLAND, W. (1903): *Eriocaulaceae*. In: ENGLER, A.: Das Pflanzenreich. Vol. 13 (IV-30). Engelmann, Weinheim.
- (1906): *Eriocaulaceae*. In: URBAN, I.: *Plantae novae andinae imprimis Weberbauerianae*. II. Bot. Jb. Syst. **37**: 519–520.
- SCATENA, V. L. (1990): *Morfoanatomia de espécies de Syngonanthus RUHL. (Eriocaulaceae) dos campos rupestres do Brasil*. Ph. D. Thesis, unpublished, São Paulo, Brazil.
- SHIELDS, L. M. (1950): Leaf xeromorphy as related to physiological and structural influences. Bot. Rev. **16**: 399–438.
- SILVEIRA, A. A. (1918): Contribuição para as Eriocauláceas brasileiras. Arch. Jard. Bot. Rio d. J. **2**: 7–8.
- (1921): *Especies novae civitatis Minas Gerais*. Arch. Mus. Nac. Rio d. J. **23**: 159–171.
- SOLEREDER, H., & MEYER, F. J. (1929): Systematische Anatomie der Monokotyledonen. 4. Gebrüder Bornträger, Berlin, 50–70.
- STÜTZEL, TH. (1984): Blüten- und infloreszenzmorphologische Untersuchungen zur Systematik der Eriocaulaceen. Diss. Bot. **71**. Cramer, Vaduz.
- (1985): Die systematische Stellung der Gattung *Wurdackia (Eriocaulaceae)*. Flora **177**: 335–344.
- (1988): Untersuchungen zur Wurzelanatomie der Eriocaulaceen. Flora **180**: 223–239.
- & BRIECHLE, M. (1990): Saugschuppen bei Eriocaulaceen – Untersuchungen zum Wasserhaushalt und mögliche Konsequenzen für die Phylogenie der Eriocaulaceen. Flora **184**: 81–89.
- TATEOKA, T., INOUE, S., & KAWANO, S. (1959): Notes on some grasses IX. Systematic significance of bicellular microhairs of leaf epidermis. Bot. Gaz. **121**: 80–91.
- TOMLINSON, P. B. (1969): *Eriocaulaceae*. In: METCALF, C. R. (ed.): *Anatomy of the Monocotyledons*. 3. Clarendon Press, Oxford, 146–192.
- UPHOF, J. C. TH. (1962): Plant hairs. In: ZIMMERMANN, W., & OZENDA, P. G. (eds.): *Handbuch der Pflanzenanatomie*. Vol. 4, part 5. Gebrüder Bornträger, Berlin, 1–205.

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Ökologie und Umweltschutz sind zu sehr aktuellen und existenziellen Problemen der Menschheit geworden. Demzufolge häuft sich die Literatur zu diesem Themenkreis. Die Zahl sehr stark generalisierender Publikationen scheint schneller zu wachsen als die Anzahl wirklich neuer empirischer Untersuchungen. Dennoch ist dieses Buch von Interesse, weil hier ein führender Vertreter der russischen Wissenschaft mit entsprechender Insider- und Literaturkenntnis seine Position formuliert. Gleichzeitig wird damit auch die sehr reiche, wegen fehlender Übersetzungen viel zu wenig international berücksichtigte Literatur zumindest ansatzweise erschlossen.

Der Autor kommt vom Staatlichen Komitee für Hydrometeorologie und Umweltkontrolle der ehemaligen UdSSR, ist also eng mit den behandelten Fragen vertraut. Seine wissenschaftliche Grundposition zum Mensch-Umwelt-Verhältnis entspricht im wesentlichen den Vorstellungen VERNADSKIJS.

In einem Einführungskapitel beschäftigt er sich mit der Frage der umfassenden Umweltanalyse und der Umweltregulation. (Wie können die Wechselbeziehungen zwischen Mensch und Natur optimiert werden, wie erfaßt man die regionale ökologische Belastung?) In diesem Zusammenhang werden solche Probleme diskutiert wie:

- hohe oder noch vertretbare Umweltqualität,
- mögliche und kritische Antworten des Ökosystems und anderer Elemente der Biosphäre auf anthropogene Einflüsse, Zustand der Ökosysteme zwischen zwei Einflußnahmen,
- mögliche und kritische Größen von Einflußfaktoren für Indi-

viduen, Populationen, Zönosen, Ökosysteme oder die ganze Biosphäre,

- mögliche Fluktuationen der Umweltqualität.

Der zweite Teil des Buches ist den Prinzipien des Umweltmonitorings gewidmet. Es werden drei verschiedene Typen des Monitorings unterschieden: geophysikalisches, biologisches und Klima-Monitoring, und Vorschläge für ein globales Monitoring unterbreitet.

Der letzte Teil beschäftigt sich mit globalen ökologischen Problemen und kritischen Schwellenwerten anthropogener Einflüsse. Es werden die verschiedenen schädigenden Wirkungen auf Atmosphäre und Klima, der Schadstofftransport über große Distanzen, die Ökotoxikologie des sauren Regens, geophysikalische und ökologische Konsequenzen eines Nuklearkrieges und die anthropogene Beeinflussung der Weltmeere behandelt.

Nicht zuletzt der Zusammenfassung merkt man den Zeitpunkt der Entstehung dieses Buches an (die vorliegende Übersetzung basiert auf der zweiten Auflage von 1984). Viele Aussagen und Interpretationen sind nur bei Berücksichtigung der zu dieser Zeit herrschenden nationalen und internationalen Situation verständlich. Einerseits ist es zwar schade, daß das Buch erst jetzt in englischer Übersetzung vorliegt, andererseits hat damit ein größerer Leserkreis Zugang zu einem auch heute noch umweltpolitisch und wissenschaftshistorisch interessanten Dokument mit immer noch großer Aktualität.

Bereits vor mehr als einem Jahr erschien die deutsche Übersetzung (IZRAEL, YU. A.: *Ökologie und Umweltüberwachung*. Jena: Fischer 1990. – 336 S., 79 Abb., 42 Tab.), auf die, in Hinblick auf sehr unterschiedliche Preise (deutsche Ausgabe nur 45,00 DM), noch hingewiesen werden soll.

S. KLOTZ, Halle (Saale)

PLACHTER, HARALD: **Naturschutz**, UTB 1563 – Stuttgart, Jena: Gustav Fischer Verlag: 1990. – 463 Seiten, 110 Tab., 99 Abb. Paperback. Preis DM 44,80. ISBN 3-8252-1563-6

„Der wirksame Schutz der Natur ist eine der größten Herausforderungen an die Menschheit“, dieser Erklärung, wie sie auf der Umschlagseite zu lesen ist, folgen nicht, wie man vielleicht vermuten könnte, allgemeine Erörterungen, sondern handfeste Argumente und Hinweise zum Handeln. Um die Hauptaufgabe, nämlich Erhaltung der Tier- und Pflanzenwelt in ihren natürlichen Lebensräumen, zu umreißen, vermeidet der Verfasser das heute viel mißbrauchte Wort „Ökologie“ und spricht von einem „biologisch orientierten Naturschutz“. Zur Begründung der Maßnahmen des Naturschutzes stellt er die ethische Verantwortung der Menschen gegenüber der uns umgebenden Natur in den Vordergrund, ohne zu übersehen, wie stark diese Aufgaben mit einer ökologisch orientierten Gestaltung unseres Lebensraums verbunden sind.

Nach einer knappen Übersicht über Geschichte und globale Aspekte des Naturschutzes widmet sich das Buch vorrangig den Verhältnissen in Mitteleuropa und dabei wieder besonders den Aufgaben in der Bundesrepublik Deutschland (vor der Wiedervereinigung). In einem ersten Hauptteil werden die verschiedenen Bereiche der Landnutzung wie Land-, Forst- und Wasserwirtschaft, aber auch Bergbau, Siedlungs- und Verkehrswesen behandelt, mit denen die Aufgaben des Naturschutzes zu koordinieren sind. Ebenso wird zu dem neuerdings stark in alle Landschaftsräume eingreifenden Einfluß von Tourismus sowie von Jagd und Binnenfischerei Stellung bezogen. Eine gedrängte Übersicht über die Geschichte unserer Natur- und Kulturlandlandschaft soll zum Verständnis des Zustandekommens der heutigen Artenvielfalt beitragen.

Aus dem Kapitel „Flurbereinigung“ ergibt sich besonders deutlich, in welchem erschreckendem Maß die Forderungen von Seiten einer technisch orientierten Landwirtschaft in den letzten Jahrzehnten zur Verarmung der Tier- und Pflanzenbestände in unserem Land beigetragen haben.

Die jeweils den einzelnen Kapiteln über Landnutzungsformen zugeordneten Abschnitte „Ziele des Naturschutzes“ vermitteln ein Bild von der Weite der Aufgaben eines systematisch betriebenen Naturschutzes. Viele Stellungnahmen sprechen dabei von einer breiten praktischen Erfahrung des Verfassers. Das gleiche gilt für die Ausführungen über die speziellen Naturschutzaufgaben, die getrennt nach Flächenschutz und Artenschutz behandelt werden. Der derzeitige Bestand von Naturreservaten, die etwa

1,7% unseres Landes einnehmen, wird kritisch bewertet im Hinblick auf Repräsentation charakteristischer Ökosysteme, Erhaltungsmöglichkeiten und Erhaltungszustand. Nachdenklich stimmt es, wenn der Autor die größere Flächen einnehmenden Landschaftsschutzgebiete und Naturparke als wenig effektiv für den Naturschutz einschätzt.

Im Zusammenhang mit einer ausführlichen Behandlung der Aufgaben einer Gebietsbewertung für spezifische Naturschutzvorhaben werden auch Ziele naturschutzbezogener Forschung herausgestellt. Die dabei geäußerte Befürchtung, daß mit dem Zerfall vieler Forschungseinrichtungen und Arbeitsgruppen der speziellen Zoologie und Botanik in Deutschland wesentliche Voraussetzungen einer effektiven Naturschutzforschung verlorengehen, kann vom Referenten voll und ganz geteilt werden.

Die in dem Buch ausführlich angesprochenen Aufgaben und Ergebnisse des Artenschutzes zeigen, daß das derzeitige Reservatsystem die Erhaltung der heute noch bestehenden Artenmanigfaltigkeit keineswegs garantieren kann. Der sich in den Roten Listen abzeichnende gravierende Rückgang an Tier- und Pflanzenarten erfordert für die Zukunft eine viel stärkere Durchsetzung der gesamten Kulturlandschaft mit naturnahen Flächen. Die Erfassung solcher oft nur begrenzter Reste naturnaher Vegetation und Tierwelt, der sogenannten Biotope, gehört zu den Aufgaben, vor denen die Naturschutzpraxis heute steht. Mit Hinweisen auf dahin zielende Länderprogramme und auf bessere Zusammenarbeit mit der Gebietsplanung orientiert das Buch über besonders brennende Aufgaben der heutigen Naturschutzarbeit.

Im Hinblick auf die bevorstehenden umfassenden Verpflichtungen, innerhalb einer ständig sich ausweitenden Zivilisation der Natur zu ihrem Recht zu verhelfen, erscheinen nach Meinung des Referenten die an letzter Stelle behandelten „Grundlagen der Gesetzgebung und der Organisation des Naturschutzes“ in der Bundesrepublik und den benachbarten mitteleuropäischen Staaten als viel zu schwache Stützen. Man wünscht den Geschöpfen der Natur stärkere Anwälte!

Es ist dem Verfasser sehr zu danken, daß er aus wissenschaftlicher Arbeit, praktischer Erfahrung und unter Beachtung einer umfangreichen Literatur (über 35 Seiten Literaturverzeichnis!) die derzeitige Situation des Naturschutzes so umfassend vorstellt.

Das Buch bietet eine gute Grundlage für praktische Naturschutzarbeit und auch für eine unbedingt notwendige vorwärtsweisende Diskussion über die dringenden Aufgaben des Naturschutzes, an der kein Biologe vorbeigehen sollte.

H. MEUSEL, Halle

Errata

- Page 403, 2nd column: Lines 49 to 51 should read ... *S. cf. pulcher*) or the abaxial (*S. xeranthemoides* and *P. flaccidus*) epidermis/hypodermis, if at all.
- Page 404, legend Fig. 2: Line 4 should read ... c) *E. modestum*, *E. sellowianum*, *S. appressus* ...
- Last lines should read ...i) *P. subulatus*. k) *S. xeranthemoides*.
- Page 405, 1st column: Lines 13 to 16 should read The distal end of the apical filamentous cell normally is acute (fig. 3; I - III), sometimes oblique (fig. 3; V) or rounded (fig. 3; IV).